Evolutionary biogeography of the Australian flora in the Cenozoic Era

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Abstract

The dominant historical pattern of the Australian flora over the last 65 million years is one of contraction of a widespread mesic flora that contained both rainforest and sclerophyll components, and expansion and diversification of dry climate and fire tolerant groups, especially sclerophyllous groups. Many species (perhaps the majority) are from lineages that have existed continuously in Australia since the final break-up of Gondwana. However, this autochthonous flora has been overlain by a complex pattern of migration into and out of Australia, including trans-oceanic dispersal among temperate southern hemisphere landmasses and across-land (or island hopping) immigration from Asia. Some major historical biogeographic patterns within Australia seem fairly clear (such as the separation of mesic zones of south western and south eastern Australia). However, many other biogeographic patterns and processes within Australia are still very poorly understood.

Introduction

Evolutionary history is important for understanding how biomes were assembled, why floras from physically similar environments in different parts of the world are composed of strikingly different taxa and why some regions have more species, endemic species or endemic clades than others.

In this chapter we aim to provide a synthetic, testable narrative of the evolution of the flora of Australia (including southern New Guinea) in space and time, concentrating on the most influential formative years prior to and after the isolation of the continent in the late Eocene. We will first review previous ideas on the evolution of the Australian flora. We will then consider the evidence that is now available on the evolution and historical biogeography of major Australian plant taxa, the major biomes to which they belonged, and the evolution of the landscapes in which they have lived.

A history of histories

Joseph Hooker's 19th Century insights

Hooker (1853) recognised that many genera and other "well marked" taxa were shared by New Zealand, temperate South America, and south eastern Australia (including Tasmania) but were found nowhere else. He believed that this "Antarctic flora" demanded a general explanation and argued that a previously continuous, ancestral Antarctic flora had been fragmented by "geological and climatic causes". This established the idea of vicariance (disjunctions caused by breaking up of past distributions, rather than dispersal across oceans or other barriers) and anticipated the idea of Gondwanic vicariance by many years. With no concept of continental drift, he postulated that previous intercontinental land connections may

have sunk beneath the waves due to geological uplift (supported, for example, by fossils of extant marine molluscs found hundreds of metres above sea level in South America), subsidence and erosion.

Charles Darwin might have been Hooker's closest scientific confidant but he disagreed strongly with Hooker's biogeographic explanation, asserting that dispersal of individual taxa across vast oceanic gaps was more likely than the movement of whole floras along hypothetical land bridges or stepping stones (Darwin 1859). Since then, Darwinian long distance dispersal and Hookerian movement of whole floras followed by vicariance have competed for the favour of biogeographers as explanations of discontinuous distributions.

Hooker (1860) then analysed the biogeography of the Australian flora. By counting the genera unique to Australia and those shared with surrounding continents he identified other major components of the flora: "peculiarly Indian" genera in the monsoon tropics, "Malayan" and "Polynesian" genera in the wet tropics; a South African connection in the south west; a European contingent in montane south eastern Australia; and a large group of characteristically Australian, predominantly sclerophyllous genera (later dubbed the "autochthonous element"). Hooker pointedly noted that the non-Australian elements were concentrated in parts of the continent that were geographically closest to their exotic relatives and that many more "peculiarly Indian" genera occurred in Australia than "Australian genera" in Asia. Hooker also noted striking differences between the floras of south eastern and south western Australia, especially the very high species richness and endemism in the south west. He speculated that the autochthonous element originated in South Africa, dispersed to south western Australia and later to the rest of the continent.

Elaborations of Hooker's biogeography, 1860-1960

In the hundred years following Hooker's analyses several botanists used similar methods and improved knowledge of the extant flora, palaeobotany and landscapes of remote parts of the continent to flesh out his ideas, often accompanied by hypotheses of centres of origin of floristic elements. Some of these ideas have endured, such as the hypothesis that a barrier to dispersal of sclerophyllous plants across what is now the Nullarbor Plain formed in the Miocene and effectively isolated the mesic floras of south eastern and south western Australia. However, most of the hypotheses form an outdated "invasion theory" that assumes that all major plant groups originated elsewhere and dispersed into Australian over a stable configuration of continents and oceans (Barlow 1981, 1994; Crisp *et al.* 1999).

Early palaeobotanists working on Australian specimens used "picture matching" similarity of fossil leaves, flowers, fruit and wood to living taxa to infer that Australia contained an implausible mixture of northern hemisphere and modern Australian groups of plants. Some of these fossil identifications have stood the test of time, but none should be accepted without critical appraisal (Hill 1988). In the 1950's, Isabel Cookson transformed Australian palaeobotany by systematically studying fossil pollen (e.g. Cookson and Pike 1954) and leaf cuticles (e.g. Cookson and Duigan 1950), backed up by detailed comparisons with living species. However, this work was constrained by the poor capacity to determine the ages of the fossils, and

limits to the understanding of the living flora. Overall, by the 1960's it was clear that some important modern Australian groups, such as *Banksia* (Plate 1A, B), *Eucalyptus, Nothofagus*, conifers, Santalaceae and Casuarinaceae had long histories on the continent.

A century after Hooker's seminal biogeographic analysis, Burbidge (1960) produced a monumental update, using similar methods, but armed with greatly improved knowledge of the Australian flora, especially in tropical and arid regions. She divided the continent into four floristic zones, three interzones and three focal areas of particular biogeographic interest. By counting the numbers of families and genera endemic to these regions, and those shared between the regions and with other landmasses, she identified floristic relationships or distributional tracks. Burbidge's tracks were consistent with Hooker's elements but she speculated in more detail about the historical processes that might have produced the tracks. For example, she argued that Eremaean taxa that have their closest relatives in the northern hemisphere invaded central Australia as strand or dune plants on the coastlines of Cretaceous epicontinental seas, and adapted to arid environments much later, during the Pleistocene.

Reinterpretation in the light of plate tectonic theory – 1960-1980

The scientific revolution that replaced the model of fixed continents with one of mobile tectonic plates (Hess 1962), thus corroborating Wegener's (1929) idea of continental drift, forced paradigm shifts on historical biogeography. Vicariance replaced long distance dispersal as the default hypothesis for explaining disjunct intercontinental distributions and Australia quickly came to be seen as a fragment of Gondwana, not an eternally isolated island continent. It was finally conceded that major plant taxa might have originated in Australia rather than having invaded it. A turning point in Australian biogeography was the work of Raven and Axelrod (1974), who fitted biogeographic narratives for many angiosperm families to a model of drifting continents. Using an essentially Darwinian approach they drew dispersal routes from centres of origin over new, dynamic paleomaps of the globe, and concluded that angiosperms originated in West Gondwana during the early Cretaceous and invaded the rest of the world from there.

Barlow (1981, 1994) then created a new synthesis of Australian phytogeography that incorporated new information about paleoclimatology and geomorphology. He concluded that the Antarctic and Autochthonous elements of the Australian flora were both parts of a Gondwanan flora inherited from the disintegrating supercontinent, and only differing in the degree to which they had adapted to Australia's changing environment over the past 65 million years. Thus, he considered that the autochthonous element had diversified and adapted to live in the expanding non-rainforest biomes, whereas the Antarctic element remained in the shrinking rainforests. He explained the Indo-Malayan element as coming from the collision of the Australian Plate with the Sunda Shelf in the early Miocene, with ensuing floristic exchange strongly biased in favour of Asian invaders over Australian emigrants.

Barlow was supported by other biogeographers, notably Johnson and Briggs (1975, 1981), who reinterpreted the history of Proteaceae, Myrtaceae and Restionaceae in the light of Gondwanic fragmentation and inferred their phylogenetic relationships. They concluded that most of the numerous taxa with overlapping distributions across Gondwanic fragments had vicariant histories, having dispersed with the landmasses themselves as the supercontinent broke up. They postulated that sclerophyllous members of the Proteaceae and Myrtaceae evolved from rainforest ancestors, starting in the early Cenozoic.

The impact of phylogenetic methodology

The phylogenetic revolution in biological systematics initiated by Hennig (1966) had profound impacts on historical biogeographic research. Until the 1980s phylogenetic background knowledge was provided almost entirely by taxonomy and the distributions and characteristics of genera or species. Groups that taxonomists chose not to name were usually ignored by biogeographers. This imposed substantial sources of error – the named taxa might not be monophyletic; only a small proportion of potential information about phylogenetic relationships was being considered by biogeographers; and genera were treated as units in quantitative analyses, even though genera are rarely equivalent in age, number of species or morphological diversity.

Phylogenies can estimate every speciation event in a clade's evolutionary history, especially when fuelled by spectacular technological advances in molecular biology. These phylogenies have enabled systematists at last to test phylogenetic hypotheses rigorously, and more recently, to estimate the ages of nodes in phylogenetic trees (Ho 2014). This in turn was the basis for the development of a number of potentially powerful ways to use this goldmine of historical information to test biogeographic hypotheses (Crisp *et al.* 2011b).

2.5 Palaeobotanical progress since 1960

Recent palaeobotanical studies have presented a moderately clear impression of the vegetation and flora of south-eastern Australia, as well as useful snapshots of other parts of the continent, for the Late Paleocene to the mid Miocene (~59 to 12 Ma [million years ago]). The subsequent period until the late Pliocene (~3.6 Ma) represents a conspicuous gap with very little plant fossil evidence, which poses problems for interpreting the fossil record because dry climates became prevalent in Australia during this period (Byrne *et al.* 2011).

Stover and Partridge's (1973) stratigraphic framework for fossil pollen and spores finally provided a means for determining the age of most plant fossil assemblages in south-eastern Australia. These ages are sometimes validated by the marine fossil record, palaeomagnetism, radioactive isotopes or other methods. With refinements, this system has been tentatively extended to other parts of Australia (see Macphail 2007).

Interpreting and identifying fossils has also improved through elaborations of Cookson's use of microfossils and the cuticles of fossil leaves, the incorporation of phylogenetic evidence and logic (e.g. Jordan and Hill 1999, Sauquet *et al.* 2009), and the use of non-taxonomic (physiognomic) fossil signals of climate (e.g. Greenwood *et al.* 2003) or vegetation structure (e.g. Jordan *et al.* 2014). Using phylogenies in identifying Australian fossils has helped overcome the problem that fossil identifications may be erroneous when based on ancestral characteristics shared among species that are not closely related (symplesiomorphy). Phylogenetic approaches are becoming more common but many fossils are still identified on the basis of overall similarity. The potential cost of demanding phylogenetically-informed identifications is that many fossils would be ignored (e.g. Sauquet *et al.* 2009) except when only used as physiognomic proxies

Recent meta-analyses and syntheses

Our knowledge of the evolutionary phytogeography of Australia has consolidated in the new millennium, with the publication of reviews and meta-analyses that have used greatly enhanced palaeobotanical and phylogenetic knowledge to test biogeographic hypotheses (Bowman *et al.* 2010, Byrne *et al.* 2008, 2011, Crayn *et al.* 2015, Crisp & Cook 2007, 2013, Hopper 2009, Kooyman *et al.* 2014, Sanmartin and Ronquist 2004, Sniderman & Jordan 2011). These studies found support for some of the general ideas postulated by earlier biogeographers but, not surprisingly, found many of them to be simplistic. The much greater accuracy and precision that detailed phylogenetic analyses provide over intuitively generated taxonomies and fossil identifications have allowed complex biogeographic patterns and processes to be disentangled to an extent that was unimaginable as recently as the 1980s.

Earth History

This section focuses on geological and climatic changes for the Paleogene and Neogene (~65 to 2.58 Ma) (Fig. 1). The subsequent period of ice ages (the Quaternary) is described by Mooney et al. (this volume).

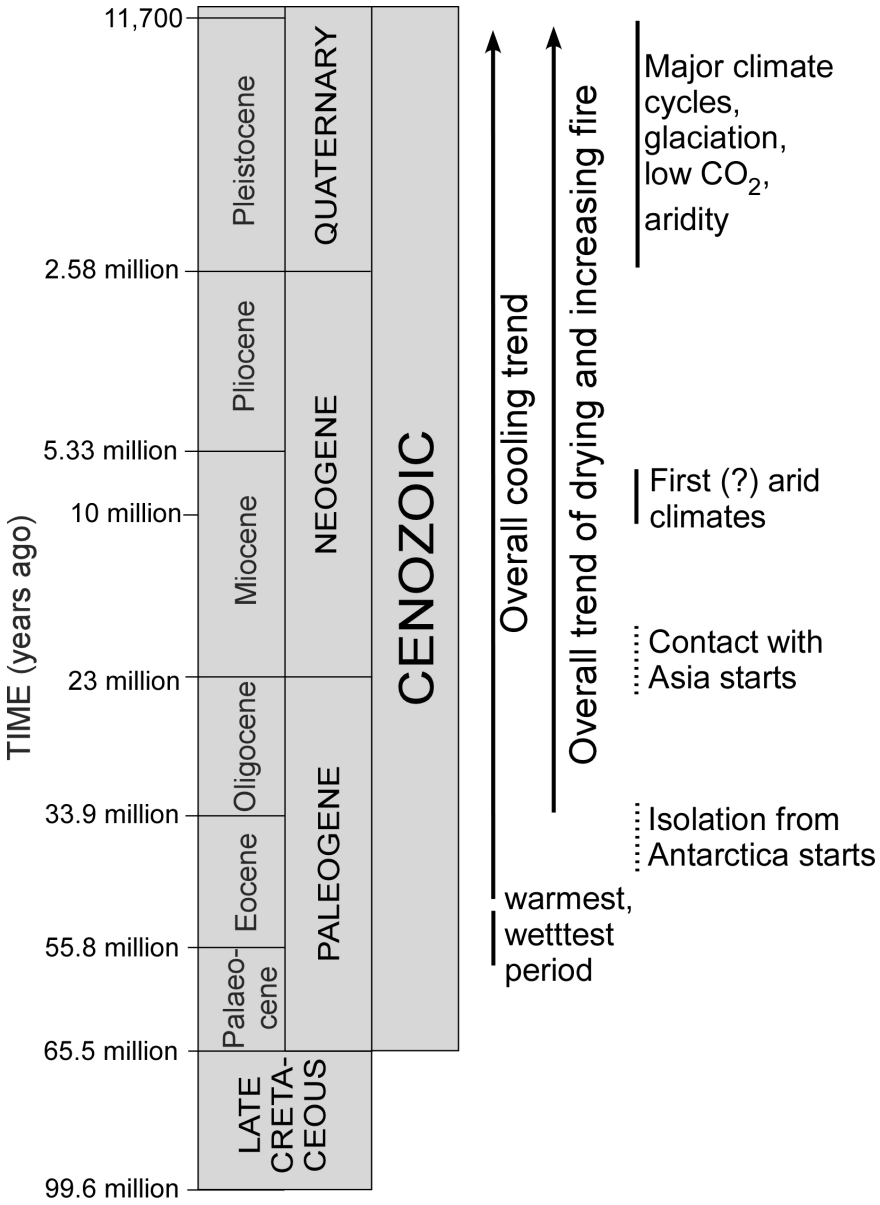

Figure 1. Geological time scale indicating the approximate ages of relevant geological periods and epochs, as well as major environmental events, as described in the text.

Historical geology

Since the beginning of the 21st century there has been general agreement about the very broad picture of the break-up of Gondwana (see McLoughlin 2001). Approximately 182 Ma, the major southern hemisphere landmasses, plus India, Sri Lanka, northern Borneo and some other fragments were connected to form Gondwana. Rifting then led to the early departure of India and Madagascar, followed by Africa in the Mid Cretaceous. Australia remained connected through Tasmania and a widening rift valley to the west. This rift valley was progressively flooded starting from the western end, creating a seaway south of Western Australia perhaps as early as Mid-Cretaceous, and increasingly isolating Australia from Antarctica except through a diminishing connection via Tasmania. That connection was severed at least 37 Ma (Exon *et al.* 2004) although a shallow water gap may have formed as early as 48 Ma (Fig. 2). On the opposite side of

Gondwana, South America remained connected or close to Antarctica until approximately the same time (Exon *et al.* 2004). The plates that now make up New Zealand, New Caledonia and a large area of land now submerged were connected to each other and attached to West Gondwana and the eastern margin of Australia. "Zealandia" probably split from West Antarctica and southern Australia ~84 Ma, but may have remained connected with north-eastern Australia until ~50 Ma (Ladiges and Cantrill, 2007). Australia's move northward led to a collision with South-East Asia ~ 25 Ma. Since then, Australia and Asia may well have been intermittently connected by land or separated by narrow seaways.

Uplift of the highlands of eastern and south eastern Australia commenced in the early Cretaceous c. 120 Ma and continued at varying rates at different latitudes until the present (Müller *et al.* 2016). In the north, the rate of uplift was almost constant, in contrast to that in the central eastern highlands and south east, where it slowed dramatically in the mid Cretaceous before accelerating in the south east during the Eocene to reach alpine altitudes in the Neogene. Uplift was accompanied by sporadic volcanism through most of the Cenozoic along an arc more or less following the Great Dividing Range from north-east Queensland to Victoria and extending to Mt Gambier in South Australia. Different regions experienced volcanic activity at different times, with eruptions until a few thousand years ago. The volcanic activities may have created disturbance regimes that facilitated the survival of disturbance-dependant taxa in periods with little or no fire. However, the major impact was the provision of fertile soils that differ dramatically from the extremely depauperate soils found across most of the continent.

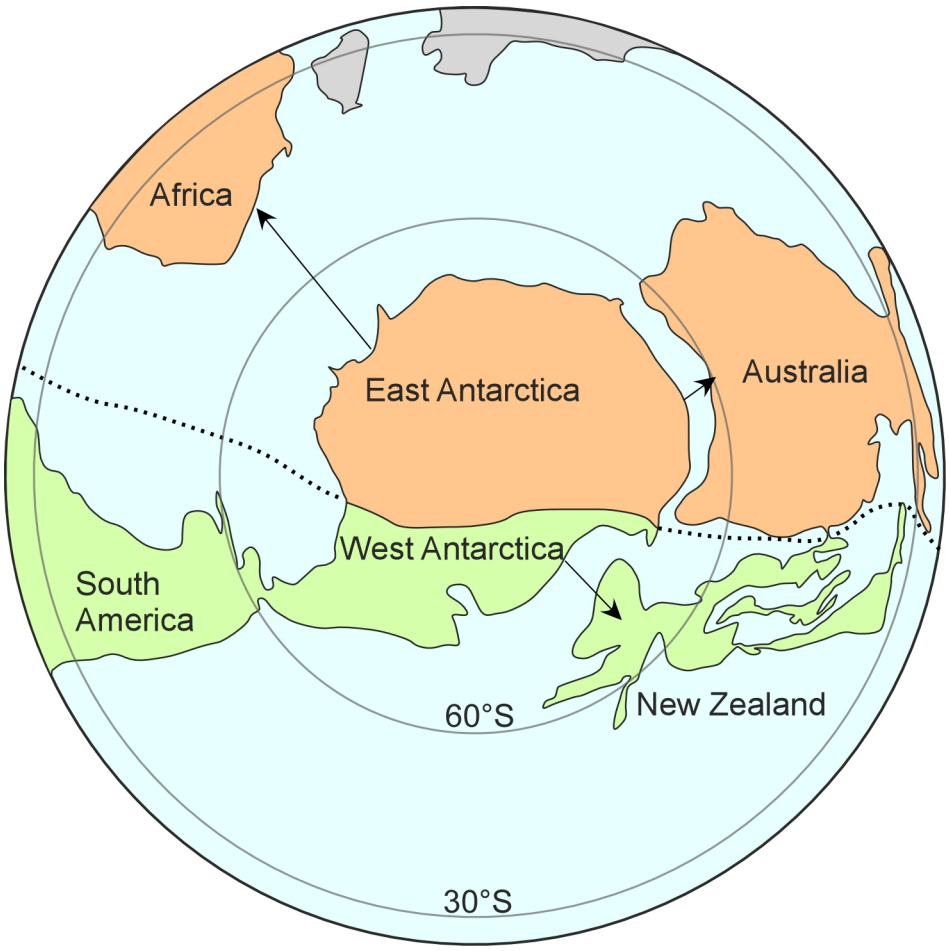

Figure 2. Gondwanan landmasses during the latest Cretaceous (~ 70 million years ago). Arrows indicate prior rifting from the rest of Gondwana. Figure based on Cantrill and Poole (2012).

Paleoclimatology

Oxygen isotopes in deep sea sediments (Fig. 3) provide a framework for understanding changes in Australia's climate over the Cenozoic. They indicate an increase in global temperatures during the Paleocene (65-56 Ma), peaking briefly at the Paleocene/Eocene boundary and then again for an extended period through the Early Eocene (~56-48 Ma). Temperatures have trended downwards ever since, with an abrupt drop at the Eocene/Oligocene boundary (~34 Ma) and partial recoveries in the Late Oligocene to Mid Miocene (~26 – 15 Ma) and Mid Pliocene (~3 Ma).

Most evidence for local terrestrial palaeoclimates comes from fossil pollen and spores (summarised by Macphail 2007). Based on this evidence, southern Australia broadly followed the global temperature trends described above. Thus there is evidence that, even at high palaeolatitudes, climates were nearly as warm as current lowland tropical climates during the Early Eocene (Carpenter et al. 2012; Pross *et al.* 2012). In addition, the major cooling event at the end of the Eocene was sufficient to create glaciers to relatively low altitudes in Tasmania (Macphail et al. 1993). Northern Australia may have shown less overall cooling since climate change was strongest in polar regions (Macphail 2007).

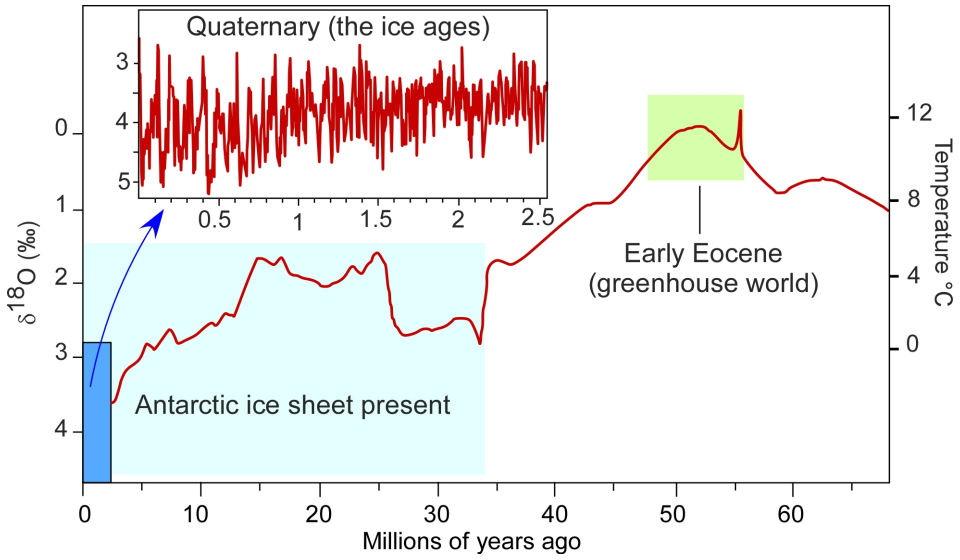

Figure 3. The oxygen isotope from fossil shells in drill cores from the deep ocean floor shows major trends in climate through time. Low values (i.e. high on the vertical axis) of delta oxygen 18 indicate a combination of globally warm temperatures and small amounts of water trapped in ice, high values indicate low temperatures and/or large ice caps. The main figure shows delta oxygen 18 for the last 65 million years, based on Zachos et al. (2001), and the inset shows delta oxygen 18 for the Quaternary (the last 2.58 million years, which includes the Pleistocene and Holocene), based on Tidemaan (1994).

The long-held view that precipitation changed in parallel with temperature still holds well for south-eastern Australia and moderately well for the rest of the continent. Thus, wet climates were present widely across Australia from the Paleocene to the Oligocene, followed by a general trend of drying (Byrne et al. 2008). Palaeoclimatic evidence for Western, Central and Northern Australia is very patchy, but the presence of mesic taxa (such as the conifers *Dacrycarpus* and *Dacrydium*) indicate that Paleocene to Oligocene climates were more-or-less mesic (although possibly less so than south-eastern Australia). Fossil *Banksia* leaves, combined with silcrete formation, suggest that south-western Australia had become at least seasonally dry by the late Eocene (Carpenter et al. 2014). Some patchy palaeobotanical evidence from North-West and Central Australia (Macphail 2007) suggests that such seasonality may have been quite widespread. Geomorphological evidence shows considerable aridification of Central Australia (and most of the rest of Australia) during the Late Miocene. A brief reversion to wet climates sufficient to support distinctly mesic vegetation on the Nullarbor Plain occurred in the mid Pliocene (~3.5 Ma) (Sniderman *et al.* 2016).

The evolution of dominant and diverse taxa

Different taxa have responded to opportunities and selective pressures in various ways, depending on luck and the features that they inherited, so it pays to consider the history of particular clades as well as that of whole biotas. Here we concentrate on dominant or particularly diverse taxa.

Conifers

The Cenozoic history of Australia's conifers can be summarised as early dominance and diversity, followed by massive depletion induced by fire and dry climates over the last 30 million years. Most groups were driven either into mesic refugia or, more often, to regional or global extinction. Indeed, conifers reached their highest species and phylogenetic diversity in the Australian fossil record in the early Oligocene, peaking at levels possibly greater than any region of the modern world.

Fossil pollen indicates that multiple lineages of Podocarpaceae (*Dacrydium*, *Microcachrys*, *Lagarostrobos* and others that probably included *Podocarpus*) occurred in all major regions of Australia in the Eocene and probably Oligocene (Macphail 2007). Macrofossils (mostly foliage; e.g. Plate 1C) show that many more genera were present in the Eocene and Oligocene than at present, especially in Tasmania (Hill and Brodribb 1999). The extent of the subsequent restriction of the family is indicated by the fact that most of the phylogenetic diversity in Podocarpaceae now resides in the wettest regions of the continent – western Tasmania and the rainforests of north-eastern Queensland. Molecular dating (e.g. Biffin *et al.* 2011) generally estimates that the most recent common ancestors of extant members of podocarp genera are considerably younger than the oldest fossils of these genera. For instance, molecular dates suggest that *Phyllocladus asplenifolius* from Tasmania diverged from its congeners in New Zealand in the late Miocene, long after the separation of Zealandia from Australia. However, unmistakeable fossil foliage of *Phyllocladus* occurs in much older sediments in both Australia (Hill and Brodribb, 1999), and New Zealand (Jordan et al. 2011), implying either that the genus became extinct in one of these regions and then recolonised, or that the molecular dates substantially underestimate the age of the group.

Like the podocarps, Araucariaceae show Gondwanan vicariance, long distance dispersal and fossil evidence (Plate 1 D,E) of a late Cenozoic retreat to scattered mesic refuges in eastern Australia (Biffin *et al.* 2010, Hill *et al.* 1999). Cupressaceae, on the other hand, include clades with contrasting stories. The inferred timing and cladistic patterns of the family's diversification are consistent with Pangaean fragmentation (Mao *et al.* 2012). The Australian taxa that are restricted to fire-free environments (*Papuacedrus*, *Athrotaxis*, *Diselma*) are relictual, showing extremely low nett diversification rates. The only clade that occupies fire-prone and arid environments is *Callitris* and *Actinostrobus*. This clade has diversified into 20 species since 50 Ma and extends over vast areas of the Australian Arid Zone.

Nothofagaceae

Numerous authors have used *Nothofagus* as a test group for understanding the biogeography of the Southern Hemisphere. In recent decades, well-supported phylogenetic trees, cladistic biogeographic analysis and molecular dating have been used to test ideas about the biogeography of the genus. Cladistic biogeographic analysis shows Australian species clustering closer to New Zealand taxa than to South American ones in two clades (Ladiges 1998). This pattern is incongruent with the understood sequence of

Gondwanic fragmentation, which predicts that Australian and South American taxa should be closest relatives. Most recently, Sauquet *et al.* (2012) used relaxed clock molecular dating to estimate ages of clades of *Nothofagus* under a wide range of calibration strategies for molecular dating. All their strategies except those assuming vicariance yielded chronograms in which disjunctions between South America and Australasia were temporally consistent with vicariance between those continents but disjunctions between Australia and New Zealand were much younger than the Tasman Sea, strongly suggesting dispersal across the Tasman Sea. Other taxa that have similar histories to *Nothofagus* include the Atherospermataceae, Monimiaceae (Renner 2005), Winteraceae (Thomas *et al.* 2014) and Elaeocarpaceae (Crayn *et al.* 2006).

Nothofagus has a rich fossil record going back to the late Cretaceous, based on morphologically distinctive fossils of its abundant, wind-dispersed and distinctive, pollen, leaves (Plate 1F) and fruit. The genus was widespread across Australia during the Paleogene. Pollen grains of subgenus *Brassospora* (which is now extinct on mainland Australia) and subgenus *Lophozonia* formed a conspicuous component of fossil pollen floras of the Murray-Darling Basin as recently as the mid Miocene, when both disappeared from the record at a time of sharply drying climate (Macphail and Truswell 1989), although *Lophozonia* returned briefly in the early Pliocene. The south-eastern Australian rainforest species, *Nothofagus cunninghamii* retreated to numerous moist refugia during glacial maxima of the Pleistocene, expanding during interglacials (Worth *et al.* 2009).

Proteaceae

The Proteaceae exemplify Barlow's (1981) idea that the autochthonous and Antarctic elements in the Australian flora are one and the same. Thus, the Proteaceae contain both elements in the form of a suite of small rainforest genera, many of which have close relatives on other continents, and a species-rich set of largely endemic sclerophyll genera. However, both groups are old - the tribes of Proteaceae, except perhaps for the Proteeae, were probably all present on what is now Australia by the Paleocene (Sauquet *et al.* 2009: fig. S1). *Telopea*, *Alloxylon*, and Australian *Lomatia* and *Orites* are "Antarctic elements" with surviving sister groups in South America. All are Paleocene or Eocene age, but some "autochthonous" groups like *Banksia* are at least as old. Fossil *Banksia* from New Zealand (Carpenter et al. 2010) emphasise the tenuous nature of the distinction between autochthonous and Antarctic elements.

Like *Nothofagus,* Proteaceae occurs on Gondwanan fragments and was long seen as showing Gondwanan vicariance (Johnson and Briggs 1975). However, again like *Nothofagus*, this view has been challenged by molecular dating analyses (Barker *et al.* 2007, Mast *et al.* 2008, 2015, Sauquet *et al.* 2009) that suggest that long distance dispersal over water may have established many disjunct distributions between Australia and other continental fragments: South Africa (Leucadendreae, Petrophileeae, Macadamiinae); South America (Macadamiinae, Gevuininae), New Caledonia (Persoonieae, Virotiinae, Gevuininae, Hakeinae), New Zealand (Persoonieae) and Madagascar (Malagasiinae). In contrast, *Lomatia* and subtribes Embothriinae and

Roupalinae are estimated to have the right age to have diversified by vicariance with the rifting of Australia from Antarctica-South America (Milner *et al.* 2015, Sauquet *et al.* 2009). Similarly, molecular dating is consistent with *Helicia* invading south-east Asia over land and narrow sea gaps.

The cohort of angiosperm groups that came to dominate Australia's vegetation in the Paleocene included at least 27 extant clades of Proteaceae (Sauquet *et al.* 2009) as well as many extinct groups (Hill *et al.* 1995). Some groups that are now restricted to rainforests of the Queensland wet tropics and/or Burbidge's (1960) MacPherson-Macleay Overlap were much more widespread during the Paleogene and Miocene than they are now. These groups include subtribe Musgraveinae (sister of *Banksia*), *Athertonia and Eidothea*. A fossil inflorescence of Musgraveinae was found in an Eocene deposit in southern Victoria (Christophel 1984), *Athertonia* occurred in several places in central Queensland and south eastern Victoria in the Oligo-Miocene (Rozefelds *et al.* 1995) and *Eidothea* is known from several fossil sites in Victoria and on the Bass Straight lslands (Rozefelds 2005). *Embothrium*, which is now endemic to South America, occurred in many parts of Australia (Macphail 2007).

The fates of proteaceous clades in Australia since the Cenozoic climatic optimum in the early Eocene are mostly stories of either adaptation to progressively more xeric conditions, often associated with rapid diversification, or ecological conservatism as rainforest trees with very low nett diversification rates and distributional contraction (figure 4). In *Banksia*, the only large clade of Proteaceae for which an almost comprehensive species level phylogeny is available, the rate of diversification accelerated in the Neogene and decelerated from the early Miocene to the Holocene (Cardillo and Pratt 2012). Two counter-acting processes may have shaped this diversification. Aridification must have driven extinction in most lineages of Proteaceae, including many sclerophyllous and xeromorphic taxa. However, this aridification also left survivors in disconnected mesic refugia, which would have facilitated allopatric speciation between the inhabitants of geographically isolated habitats. The only clades that penetrated deep into the arid zone are several groups of *Hakea* and *Grevillea*. These groups diversified to a moderate extent, with some species establishing very widespread distributions (Mast *et al.* 2015).

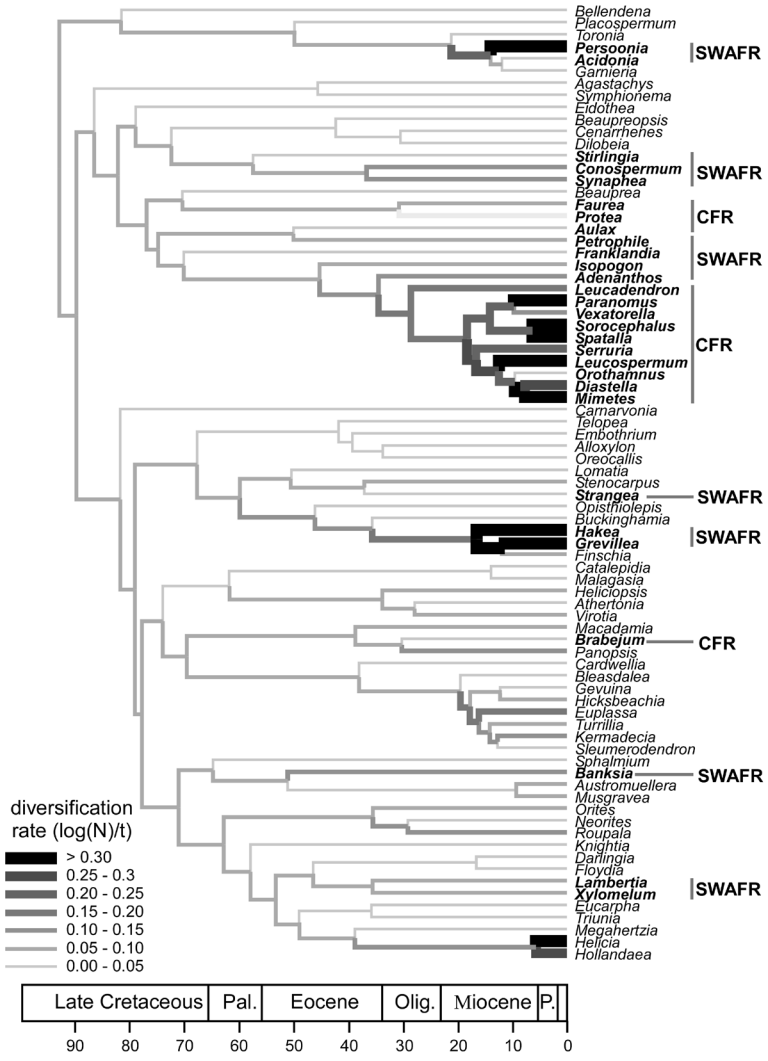

Figure 4. Molecular chronogram for the genera of Proteaceae, produced using the Bayesian uncorrelated lognormal method (implemented in BEAST) from an alignment of nucleotide sequence data for eight loci (Sauquet *et al.* 2009, Fig. 1, redrawn with permission of the senior author). Branches are toned according to absolute nett diversification rate by stem age of their subtending clade. Taxa present in Mediterranean biodiversity hotspots are identified with either SWA (south-western Australia) or CFR (Cape Floristic Region). Absolute ages are in million years.

Myrtaceae

According to the most recently published molecular chronogram of the Myrtaceae (Thornhill *et al.* (2015), the family diverged from its African sister group, the Vochysiaceae, in the mid-Cretaceous, as Africa rifted from the remainder of Gondwana. Myrtaceae largely differentiated on the fragmenting continental block of Zealandia-South America-Antarctica-Australia during the Cenozoic. A beautiful demonstration of this is provided by exquisitely preserved and precisely dated macrofossils of *Eucalyptus* of Early Eocene age from Patagonia (Hermsen *et al.* 2012).

Five extant Australian myrtaceous lineages survived the Cretaceous-Paleogene boundary (Thornhill *et al.* (2015). The family diversified quickly during the Eocene, by the end of which 34 extant Australian clades had differentiated, including 5 major clades of eucalypts (Thornhill *et al.* 2015). Diversification of

Eucalyptus accelerated through the Oligocene (Crisp and Cook 2013), as Australia's climate cooled and dried, and then – in a similar pattern to that in *Banksia* – decelerated from the mid-Miocene to the present when much of the continent became dry, presumably eliminating many species from central Australia and forcing a few lineages to adapt. Comparing the number of extant species of the two main clades of the eucalypts illustrates the strikingly higher nett diversification of the sclerophyllous clade (about 930 species) over its rainforest sister group (4 species) by the end of the Cenozoic, in a drying and fire-prone environment. The fossil record is consistent with these patterns, but at present the capacity to differentiate fossils of different groups is limited (Thornhill and Crisp 2012).

Fabaceae

The Australian legume flora is dominated by two large, endemic or nearly endemic clades dominate the legume flora of Australia: the egg and bacon peas (tribes Mirbelieae and Bossiaeeae) and *Acacia*. However, the flora contains a number of other smaller clades of Fabaceae with diverse histories (in genera such as *Archidendron*, *Senna*, *Indigofera*, *Glycine* and *Desmodium*).

The age of the diversification of the Mirbelieae-Bossiaeeae clade was estimated by Lavin *et al.* (2005) to be 48.4 ± 1.3 Ma, old enough to have inhabited the Australia-Antarctica-South America supercontinent, although the origin of the clade is difficult to determine. Lineage through time plots for the clade are consistent with diversification through the Eocene, followed by a mass extinction at about the Eocene-Oligocene boundary (Crisp and Cook 2009), when the climate cooled dramatically (Exon *et al.* 2004). The clade is now widespread across Australia, but most diverse in the temperate to subtropical south.

Acacia is much younger than Mirbelieae-Bossiaeeae, having started diversifying in the early Miocene, 23 Ma (Miller *et al.* 2013). Its closest relative is *Paraserianthes lophantha*, which has one subspecies restricted to south western Australia and one in Indonesia (Brown *et al.* 2011). Since diverging from *Paraserianthes*, *Acacia* has proliferated into almost 1000 species. This striking disparity between genera can be partly explained by numerous lineages of *Acacia* adapting to desert environments at various times during the Neogene and the failure of *Paraserianthes* to adapt to aridity. However, *Acacia* has also diversified spectacularly in the sclerophyllous communities of south western Australia, where *Paraserianthes* is native. It is not clear whether the characteristic phyllodes of *Acacia* acted as a "key innovation" in this explosive radiation.

Asterales

Phylogenetic evidence indicates that Goodeniaceae diverged from Asteraceae plus Calyceraceae clade in the Cretaceous or Paleocene, when Australia and South America where still connected to Antarctica by dry land, and started to diversify in the Eocene (Beaulieu *et al.* 2014; Jabaily *et al.* (2014). The Goodeniaceae seems to have been restricted to Australia until the late Miocene, after which two lineages of *Goodenia* and four of *Scaevola* dispersed out of Australia. Diversification accelerated in the family in the Miocene with

many events of colonisation of the arid zone, which may even have served as a "stepping stone" allowing expansion of clades between the mesic regions of southeastern and southwestern Australia via ancestors in the arid zone.

The Asteraceae first diversified in South America, then a lineage dispersed to Africa, probably in the mid-Eocene, and diversified explosively there (Funk *et al.* 2009, Barres *et al.* 2013). Almost half of Australia's 1000 or so species of Asteraceae belong to a single clade within the tribe Gnaphalieae that dispersed from Africa less than 16 Ma (Nie *et al.* 2016). The other major clade of Asteraceae in the Australian flora is the tribe Astereae, which includes about 300 native species, including *Brachyscome* and the polyphyletic *Olearia*. These taxa diversified from at least two dispersal events into Australia from unknown locations (Cross *et al.* 2002, Jafari *et al.* 2015). Both Gnaphalieae and Astereae have adapted to all the terrestrial biomes of Australia and New Zealand. Some smaller Australian clades also appear to have originated in Africa. The widely overlapping distributions and relatively young age of many closely related genera within Gnaphalieae, Astereae and other clades suggest very complex histories within this group, involving successive rounds of range expansion and allopatric diversification and dispersal to (and possibly back from) New Zealand.

Poaceae

Molecular studies agree that the most recent common ancestor of the Poaceae lived in a moist, closed habitat during the Paleocene or late Cretaceous (Bouchenak-Khelladi *et al.* 2010, Christin *et al.* 2014). Multiple clades successfully adapted to live in dry, open habitats during the late Eocene to Miocene (Bouchenak-Khelladi *et al.* 2010). Diversification accelerated and C_4 photosynthesis evolved at least 15 times between 32 and 3 Ma, as climates cooled and dried and open habitats expanded (Christin *et al.* 2008).

Ancestral area reconstructions suggest that Australian grasses arrived by multiple dispersal events during the Miocene, either from Asia, as Australia approached and collided with it, or across wide ocean gaps (Bouchenak-Khelladi *et al.* 2010). This result is consistent with the Australian fossil record, in which grass pollen (some of which may be misidentified Restionaceae) is extremely rare until the late Oligocene (Macphail and Hill 2002). After this, it becomes steadily more abundant, and by the Pliocene and Pleistocene is often the dominant pollen type, especially in dry regions (Macphail and Hill 2002). Phylogenies of two clades that are important in Australia indicate immigration into Australia via long distance dispersal. Thus, the small, warm-temperate subfamily Danthonioideae apparently followed an intricate scenario of repeated instances of long distance dispersal across the Pacific and Southern Oceans during the Miocene, with *Rytidosperma* being derived from long distance dispersal from southern Africa (Linder *et al.* 2013). The Australian species of *Poa* fall within a clade that otherwise occurs from Alaska to

Chile (Gillespie *et al.* 2007). Their divergence has not been dated but inspection of branch lengths suggests that the Australian and American taxa are too recently diverged to be vicariant.

Triodia, the dominant understory taxon in over 30% of arid and monsoon tropical Australia, diverged from its closest relatives in Asia, Europe and Africa in the early Miocene and started to diversify during the mid Miocene aridification of Australia (Toon *et al.* 2015). *Triodia* may well represent a case of an arid-adapted grass that immigrated initially into southern Australia then spread northwards as the climate dried.

Amaranthaceae

The family Amaranthaceae (including Chenopodiaceae) has a similar history to the grasses in that it originated around the Cretaceous-Paleogene boundary (Magallon *et al.* 2015), had multiple origins of C_4 photosynthesis, and only really diversified in Australia after the onset of severe aridity in the mid Miocene. Cabrera *et al.* (2011) and Kadereit *et al.* (2005, 2006, 2010) suggest that at least ten lineages dispersed independently into Australia, into arid and/or saline habitats similar to those occupied by their colonising ancestors. Only the monotypic genus *Scleroblitum* is old enough, according to molecular dating analyses, to have originated from its closest relatives by vicariance with South America. However its biogeographic history remains obscure because its closest relatives are widely distributed. Other Australian clades range in age from 23 to 1.7 Ma. Pollen grains consistent with the Amaranthaceae did not become common in Australian palynofloras until the late Miocene, when the Australian clades of *Atriplex* and tribe Camphorosmeae were rapidly diversifying.

The largest Australian group (12 genera and 147 species) is a clade that includes *Maireana* and *Sclerolaena* (Cabrera *et al.* 2011). This clade arrived in Australia in the mid-Miocene, probably from semi-arid to arid parts of Eurasia but did not start to diversify until the late Miocene, about 7Ma. Ancestral area analysis suggests the clade first took root in south western Australia and then spread to central, then eastern, then northern Australia (Cabrera *et al.* 2011). Most of Australia's 57 native species of *Atriplex*, all of which have C_4 photosynthesis, diversified rapidly from a species that arrived from central Asia in the Late Miocene, although a few species evolved from a slightly earlier immigrant (Kadereit *et al.* 2010).

Synthesis: A historical narrative

Although the biogeographic histories of individual clades often include some striking idiosyncrasies, several general historical patterns shine through. These generalisations fit in well with our knowledge of earth history and are the subject of our concluding section.

The antiquity of rainforests, sclerophylls and fire adaptation

A range of earlier authors asserted that when Australia was part of Gondwana, the landscape was dominated by rainforest. However, fossils from the Paleocene (65-55 Ma) show that Australia carried predecessors of some conspicuously different components of the modern flora, including groups

characteristic of rainforest (e.g. leafy Lauraceae), groups characteristic of sclerophyll communities (e.g. *Banksia* and probably *Eucalyptus*) and groups that span these habitats (e.g. Casuarinaceae and Loranthaceae). In fact, the oldest compelling fossil evidence for "modern" vegetation types is somewhat older (latest Cretaceous) and shows distinctly sclerophyll vegetation (Carpenter et al. 2015).

Eucalyptus and Proteaceae shed specific light on the deeper history of rainforest and sclerophyll components of the flora. Meristematic strands deeply embedded in xylem enable most eucalypts to resprout after fire, and are likely to contribute to the eucalypts' current success in fire-prone Australia. However, the very early evolution of this innovation challenges the view that fire only become significant in the last 25 million years (e.g. Martin 1996; Kershaw et al. 1994). Dated ancestral state reconstruction implies that the *Eucalyptus-Corymbia-Angophora-Arillastrum* clade had these buds at least 60 Ma, during the Paleocene (Crisp *et al.* 2011a). This corresponds well with evidence of abundant charcoal in Cretaceous deposits, mainly of the northern hemisphere (Bond and Scott 2010). *Eucalyptus* may well have been in Australia at that time – some ambiguous pollen fossils (Thornhill and Crisp, 2012) suggest that this is so, but impressive fossils show that it was in South America in the Early Eocene (Hermsen et al. 2012).

Ancestral character state reconstructions have shown that, within the Proteaceae, xeromorphic adaptations, adaptations to fire, and anatomical structures that make leaves sclerophyllous all evolved repeatedly (Jordan *et al.* 2005, 2008; Lamont and He 2012). Lamont and He (2012) further argued that the pattern of evolution of fire adaptations suggested that at least some Proteaceae became adapted to fire in the Cretaceous, long before the generally accepted increase in fire in the Neogene. These inferences have been confirmed by fossilised sclerophyllous, proteaceous leaves from a late Cretaceous deposit in central Australia that contains charcoal. The fossils closely match leaves of *Banksia*, *Stirlingia, Isopogon, Conospermum* and the tribe Persoonieae (Carpenter *et al.* 2015). However, ancestral state reconstructions of the preferred habitat of the most recent common ancestor of the Proteaceae, which lived in the Mid Cretaceous, are equivocal.

In contrast, the very warm and wet Early Eocene does show widespread fossil evidence for rainforest and little for sclerophyll floras. Widespread rainforest continued to exist even as temperatures declined during the Middle and Late Eocene, though extinctions did occur – such as numerous Proteaceae and the global last gasp of Corystosperms (extinct gymnosperm "seed ferns") (McLoughlin et al. 2008). In addition, some of the dominant groups through this period are no longer in Australia, but are now found in places such as New Zealand, New Guinea and/or New Caledonia (e.g. a suite of conifers, *Nothofagus* subgenus *Brassospora*, *Beauprea* and Strasburgeriaceae). Lactoridaceae represents a remarkable case of being stranded on a desert island (Robinson Crusoe Island).

Immigration and dispersal

Although much of the mesic flora of Australia is descended from lineages inherited from Gondwana (Sanmartin and Ronquist 2004, Kooyman *et al.* 2014), many disjunct clades with apparently Gondwanan distributions seem to have dispersed around the southern hemisphere (including dispersal in and out of Australia) across large ocean gaps after Australia's connection to Antarctica was severed (Crisp *et al.* 2009, figures 5 and 6). In addition to examples described above, there is evidence that, although the disjunctions between Australasian and South American epacrids resulted from vicariance, many clades of Ericaceae have dispersed between Australia, New Zealand and New Caledonia quite recently (Puente-Lelievre et al. 2013; Schwery et al. 2015; Wagstaff et al. 2010). This included regional extinctions and recolonisations (Jordan et al. 2010; Puente-Lelievre et al. 2013). Dispersal of tropical taxa from Asia into Australia's wet tropical and monsoonal biomes dates back at least to 33 Ma but the rate of immigration accelerated about 12 Ma as the Sunda and Sahul shelves came in to close proximity, with a strong bias towards immigration over emigration (Crayn *et al.* 2015, Sniderman & Jordan 2011).

Aridification and the increase in fire

Although there has been a long-held view that aridification of Australia commenced in the Miocene, parts of Australia appear to have had relatively dry climates earlier than this, with Late Eocene rocks in south western Australia containing fossil leaves of *Banksia* that are clearly xeromorphic and not just scleromorphic (Carpenter et al. 2014). The scarcity of plant fossils outside south-eastern and eastern Australia may also be a sign that other parts of Australia had dry climates unsuited to preserving plant fossils. Thus, some habitats in central, northern and western Australia may well have been dry enough for xeric lineages to persist through even the very wet Early Eocene.

Notwithstanding the previous comments, the Australian fossil record indicates that climates dried, fire-dependent groups (such as eucalypts, Asteraceae and grasses) and charcoal increased, and rainforest contracted (Kershaw *et al*. 1994) during the Neogene. A wide range of molecular evidence supports the idea that the arid zone expanded and Eremaean taxa diversified in that period (Byrne *et al.*, 2008). This evolution of the arid zone flora included *in situ* adaptation, dispersal from more mesic environments, and long distance dispersal of already xeric taxa from other continents (Byrne *et al.* 2008).

Figure 5. Vicariance and long distance dispersal among the austral floras, derived from the data set of Crisp *et al.* (2009). The first value gives the number of disjunctions in sampled taxa assigned to vicariance, the second the number of disjunctions attributed to dispersal. The line thickness indicates the proportion of disjunctions attributed to vicariance. Figure redrawn with permission from one by H. Peter Linder.

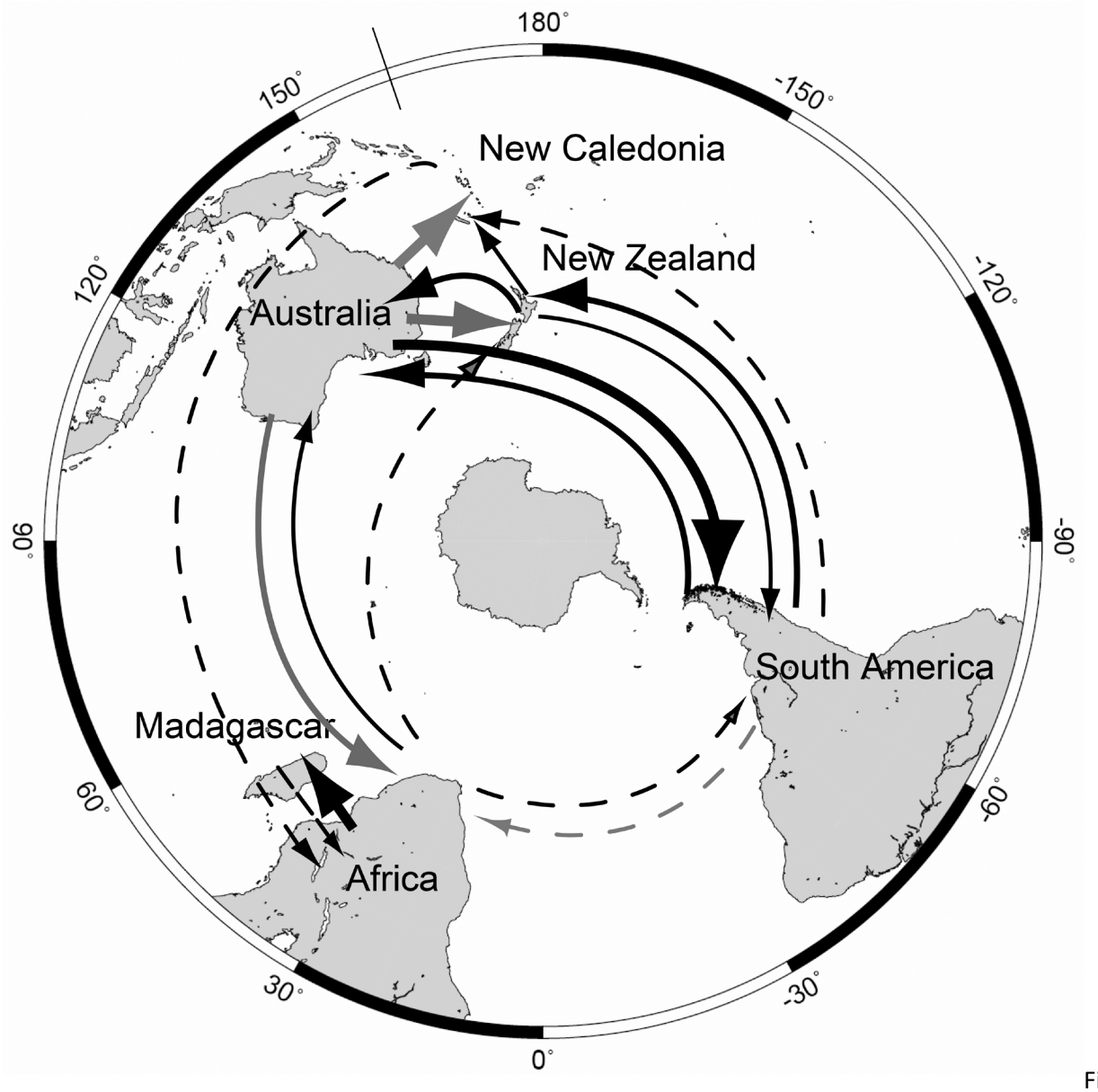

Figure 6. The number of colonisation events among the austral floras, derived from the data set of Crisp *et al.* (2009). Arrows indicate the number of colonisation events: broken lines, less than 2 events, thin solid lines 2-5 events, next thickness 5-10, then 10 to 20, and thickest lines more than 20 colonisation events. Figure redrawn with permission from one by H. Peter Linder.

Rainforest and other mesic groups became increasingly restricted to a sparse archipelago of well-watered areas separated by barriers to dispersal and gene flow (Byrne *et al.*, 2011). Although this fragmentation probably induced some evolution and speciation in rainforest clades, rates of diversification (net speciation) are considerably greater in relatively dry habitats in the South West Floristic Region, eastern Australia and the arid zone (Fig. 4; Crisp *et al.* 2009, Byrne *et al.* 2011). Thus, relative to their ages, dry climate and sclerophyll lineages are generally more species-rich than rainforest lineages (Crayn *et al.*, 2006; Sauquet *et al.*, 2009).

Geographic splits within the sclerophyll flora.

The most spectacular biogeographic barrier in Australia is the Nullarbor Plain. This barrier appears to explain many of the numerous east-west disjunctions, especially in sclerophyllous plant groups, with a distinct peak in age estimates of disjunctions between 10 and 15 million years ago, the inferred time of formation of the barrier (figure 7; also Crisp and Cook 2007). A few disjunctions, such as that between the major eastern Australian clade of *Eucalyptus* subgenus *Eucalyptus* and its closest western relatives (Crisp *et al.*, 2004), and in *Banksia* (Crisp and Cook 2007), are older (Oligocene). Ladiges *et al.* (2011) argue that such distributions (including disjunctions in *Corymbia* and *Eucalyptus* subgenus *Eudesmia*) may have been bisected by drying at the Oligocene-Miocene boundary. The barrier is not complete, with numerous (and presumably relatively recent) disjunctions within species across the barrier, and fossil evidence for relatively mesic habitat in heart of the Nullarbor since the main formation of the barrier (Sniderman *et al.*, 2016).

Similarly, some disjunctions between northern and southern/eastern Australia seem to relate to aridification. In both *Corymbia* and *Eucalyptus* subgenus *Eudesmia*, species endemic to the Top End and Kimberley regions are more closely related to eastern species than to those in the south west (Ladiges *et al.* 2011). Also, both *Corymbia* and *Eudesmia* show intricate patterns of diversification within the arid zone, implying that the arid zone is not homogenous in biogeographic terms, but acts as a highly dissected landscape.

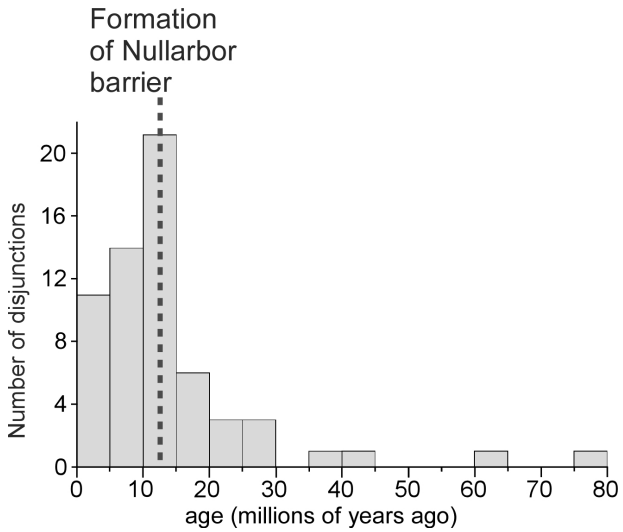

Figure 7. Dated disjunctions in plant taxa between mesic areas of south western Australia and eastern Australia. Note the spike in number of disjunctions at the time of formation of the Nullarbor Plain barrier, and also that many disjunctions are younger than this. Data come from published chronograms of *Grevillea/Hakea*, *Banksia*, Fabaceae, Ericaceae, Restionaceae, Goodeniaceae, Rhamnaceae, Colchicaceae, Casuarinaceae, conifers, Asparagaceae, Anarthriaceae and Haemodoraceae.

Other biomes.

The history of the alpine flora can be broadly split into very distinct groups. One small component of the alpine flora focussed on the western Tasmanian mountains has very deep history, containing a globally significant suite of palaeoendemic clades, including early diverging endemic, or nearly endemic genera of conifers, Proteaceae and monocots (Plate 1 G,H) (Jordan et al. 2015). However, most alpine species belong to young and very widespread clades, often being distributed widely across the southern hemisphere, such as several clades of daisies (e.g. Wagstaff *et al.* 2006), genera of Cyperaceae and other herbs, or even globally, such as *Poa* and Danthonioid grasses (e.g. Gillespie *et al.* 2007, Linder *et al.* 2013). Some of these alpine plants appear to represent in situ evolution from lowland clades (e.g. *Grevillea* species; Mast *et al.* 2015). This recent origin probably reflects the relatively recent creation of alpine habitat in Australia by cooling climates combined with geological uplift (Müller *et al.* 2016).

The history of the monsoon biome remains relatively unclear, with most evidence summarised by Bowman et al. (2010). It appears to have included multiple immigrations of monsoon clades, especially from Asia (Crayn *et al.* 2015), although some clades (e.g. within Proteaceae – Mast *et al.* 2015) are autochthonous. There is some evidence for a mid Miocene origin of several Australian savanna clades (Toon *et al.* 2015).

Conclusions

Overall, this historical narrative is patched together based on still fragmentary evidence, and all aspects are open to testing. Many of the main components of this story have enough support that they have a good chance of standing the test of time, but all are subject to change as evidence accumulates, methods improve and paradigms shift.

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